

## NOTES ON THE MORPHOLOGY OF THE EYES OF COLEOPTERA\*

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### I. OCELLI

Ocelli occur in adult Coleoptera as follows: a pair of ocelli in the Omaliini (Oxytelinæ, Staphylinidæ) ("un Oxytelide american (*Trogophlaeus argus*)" (Houlbert, 1921, *Col. Europe France* I, p. 25) is listed in recent catalogues under Omaliini as *Phloeonomus lapponicus* Zett.) and in certain species of the primitive Silphinæ as *Pteroloma forstræmi* Gyllh., and *Camioleum loripes* Lew. (Fowler, 1912, *Fn. Br. Ind.*, p. 84); a single median ocellus in the tribes of Dermestidæ (Dermestini) exclusive of Dermestini and in *Phlaeobium clypeatum* Muell., (Proteinini, Oxytelinæ, Staphylinidæ). These structures are located on the vertex of the epicranium between or slightly behind the compound eyes, and, if they are true ocelli, require that the three ocelli of the primitive insect be inserted on the vertex in Stickney's figure of the head of the hypothetical coleopteron (1923, *Ill. Biol. Mon.* VIII, plate I, fig. 1).

### II. DIVIDED EYES

There are ten unrelated groups of Coleoptera, representing six families that have the eyes completely divided. The morphological condition is the same throughout. As the eye is constricted the portions of the oculata (ol, figs. 8, 9) in the region of the constriction are brought together, and, in the completely divided eye, meet to form a suture, the exoculata (eo, figs. 1-8) connecting the faceted areas. In the region of the exoculata the oculata is somewhat narrower than about the margins of the faceted areas, but it is still present as an entad extending parademe. The complete division of the compound eye is only the consummation of the emargination of the eye that is of such frequent occurrence in Coleoptera.

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There are about three general types of divided eye.

I. Associated with a caudad movement of the antenna: (1) *Euderces pini* Oliv., (fig. 1) and *E. reichei* Lec., (Cerambycinæ) and (2) *Tetraopes* (fig. 2) and the closely related *Tetrops* (Lamiinæ) among the Cerambycidae.

II. Associated with a caudad extension of a canthus across the eye: (1) *Scarabæus* and other Scarabæinæ and (2) *Geotrupes* (fig. 3) and other Geotrupinæ among the Scarabæidae.

III. Associated with a caudad movement of the frontal ridge, directly underneath which is the antenna, which either may not: (1) *Polygraphus* (fig. 4) (Hylesininæ) and (2) *Xyloterus* and its allied genera, *Xyloterinus* (fig. 5) and *Trypodendron* (Ipinæ) among the Ipidæ, or may be correlated with a caudal emargination of the eye: (3) *Blapstinus* (fig. 6) and other genera among the Pedininæ and (4) the Opatrinæ (Tenebrionidæ), (5) *Amphiops* (fig. 7) (Hydrophilidæ) and (6) Gyrinidæ (fig. 8).

I. The first mentioned condition is the most common. *Chariessa* (Corynetidæ), *Trypitiium* (Cephaloidæ), *Nacerda* (Oedermeridæ), and *Epicauda* (Meloidæ) are more or less unrelated examples of the slightly emarginate condition. *Euderces pini* Oliv. and *E. reichei* Lec. (Leng, 1887, Ent. Am. III, p. 24) among the Cerambycinæ and *Tetraopes* and *Tetrops* among the Lamiinæ stand independently at the end of long cerambycid series exhibiting all degrees of emargination. In these forms the antacava is between the portions of the eye, and the exoculata is homologous in position with the narrowed isthmus of the eye in related types. In *Tillomorpha geminata* (Hald.), closely related to *Euderces*, the dorsal eye is said to have disappeared entirely, leaving only the lower eye (Leconte and Horn, 1883, Class. Col. N. A., p. 305). In *Euderces picipes* Fab. the two lobes of the eye are still connected by such an isthmus, containing facets (not devoid of them as stated by Leconte and Horn, *ibid.*, p. 306) showing the phylogenetically recent occurrence of the division. *Tetropium* (Cerambycinæ) is another unrelated cerambycid in which the eye is not completely divided, but in which the isthmus is devoid of facets, bringing about a physiological condition similar to that in the forms with double eyes.

II. A more or less extensive canthus projecting from the cephalic margin of the eye is found in *Throscus* (Throscidæ) and

is nearly universal among the lamellicorns (absent in *Ceruchus*, a lucanid). At times, as in *Throscus* and many Melolonthinæ, the canthus is devoid of a ridge, but in the other groups there is present on it a prominent ridge that is a portion of the lateral margin of the head. The eye is completely divided in a series of geotrupine (*Odontæus*, *Geotrupes* (fig. 3), *Ceratophyus*, *Lethrus*) and scarabæine (*Phanæus*, *Scarabæus*, *Oniticellus*, *Bubas*, *Onitis*) genera, and the two portions are respectively dorsal and ventral.

III. Closely related to the first condition is the third, with the addition of a frontal ridge dorsad to the antacava. The simplest condition is illustrated by the double-eyed Ipidæ, in which there is no caudal emargination of the eye. *Crypturgus* (Hylesininæ) among the genera related to *Polygraphus* and *Monarthrus* (Ipinæ) among the genera related to *Xyloterus* exhibit an emargination of the cephalic margin of the eye. The males of *Xyloterus* have the frontal ridge strongly developed so that the two portions of the eye are dorsal and ventral; in the others the frontal ridge is feebly developed.

In the double-eyed tenebrionids, in *Amphiops*, and in the Gyrinidæ the exoculata does not connect the caudal margins of the divided eye as in all the groups so far mentioned, but it traverses the middle of the interocular area showing that the eye has become divided as a result of an emargination on both cephalic and caudal margins. The cephalic emargination is correlated with the caudad extension of the frontal ridge, as in the Ipidæ, causing the portions of the eye to be dorsal and ventral respectively. The caudal emargination is correlated with the cephalic encroachment of the anterior angles of the pronotum along the sides of the head.

Among the Tenebrionidæ (fig. 6), numerous genera of Pedininae (all the genera of Blapstini: *Ulus* through *Coniobiosoma* in Leng, 1920, Cat. Col. Amer., pp. 233-234, *Pedinus*, *Colpotus*, *Cabirus*, *Isocerus*, *Heliophorus*, and perhaps others, Reitter, 1904, Best.-Tab. 53, pp. 50, 77, Lacordaire, 1859, Gen. Col. V, p. 244) and numerous genera of Opatrinae (all the genera of the subdivision Phylacina, Reitter, *ibid.*, p. 106-107). Incipient stages of this division are exhibited by Alleculidæ, Tenebrionidæ, La-

griidæ, and Melandryidæ, all related families. Most of these (*Melandrya*, *Penthe*, *Merinus*, etc.) exhibit only an emargination of the cephalic margin. *Opatrinus* exhibits an emargination of both margins.

The emargination of the caudal margin of the divided eye of *Amphiops* (fig. 7) is well developed in the Hydrophilini, but the cephalic margin is practically entire throughout the family Hydrophilidæ except in the Sphæridiini, where both margins are emarginate.

The Gyrinidæ (fig. 8), all of which have the eye divided, represent the culmination of double-eyed development in Coleoptera and are the only group in which this feature appears to be related to the life habits of the animal. The early stages of this process are, perhaps, exhibited by the Colymbetinaë (Dytiscidæ) which exhibit a definite notching of the anterior margin of the eye by the frontal ridge as well as a slight emargination of its caudal edge (fig. 9). All that is necessary to transform such an eye into a gyrid eye is to extend the epicranium (dotted lines "x," fig. 9) over its middle portion. The distinct relationship between the two families makes such an homology possible. The two portions of the gyrid eye are widely separated and, when seen in lateral view, present more or less parallel margins to each other. Extending from the anterior-ventral margin of the dorsal eye to the anterior dorsal corner of the ventral eye is the exoculata.

The males of *Dioptoma* (fig. 10) (Rhagophthalmini, Telophoridaë) do not have the eye divided as intimated by Sharp (1899, Camb. Nat. Hist. VI, p. 251) but have it somewhat constricted and traversed by a distinct sulcus, and the dorsal lobe divided by a lesser sulcus into anterior and posterior lobes. The facets vary in size: the smallest are in the sulcus, the next largest are in the posterior dorsal lobe, the next largest in the anterior dorsal lobe, and the largest in the ventral lobe, which covers most of the venter of the head.

In certain may-flies likewise (Comstock, 1920, Intro. Ent., p. 144) where the eye is divided the facets of the lower eye are said to be larger than those of the dorsal eye. This variation is correlated with a difference in the internal structure of the ommatidia

adapting the upper eye for day vision or vision in bright light and the lower eye for night vision or vision in dim light and the same may be suggested for *Dioptoma*, though its habits are unknown. While the lower portion of the eye in the other forms mentioned above is more extensive than the dorsal, no variation in the size of the facets is detected. It does not appear, however, that the distribution of pigment between the ommatidia making for day or night vision is always or even usually correlated with differences in the size of the facets, and in many eyes, as in *Colymbetes*, the pigment cells appear to migrate under the stimulus of light so that the same ommatidia may function as day eyes in strong light and night eyes in weak light (Comstock, *ibid.*, pp. 142-144).

Some of the early authors described and figured a divided eye in *Adelotopus* (Carabidæ, Pseudomorphinæ) (Hope, 1836, Tr. Ent. Soc. London I, plate I, fig. 1b; Lacordaire, Gen. Col. I, 1854, p. 153, and plate V, fig. 4 bis; Sharp, 1868, Ent. Mo. Mag. V, p. 52). Horn (1867, Tr. Am. Ent. Soc. I, p. 152) indicated that this was an erroneous observation, and this is substantiated by Westwood's figure (1853, Rev. et. Mag. Zool. (2), V, plate 15, fig. 2b) and reference to the single specimen in the author's collection (fig. 11). The eye is situated entirely on the dorsal aspect of the head and appears quite homologous with the dorsal eye of *Blapstinus* or a gyrid. Comparison with *Silphomorpha* shows that is probably not the case, but rather that it is the end result of the gradual migration of the eye from the side to the top of the head. The question of the mimicry of Gyridinæ by *Adelotopus* (Sharp, *ibid.*), therefore, is not raised.

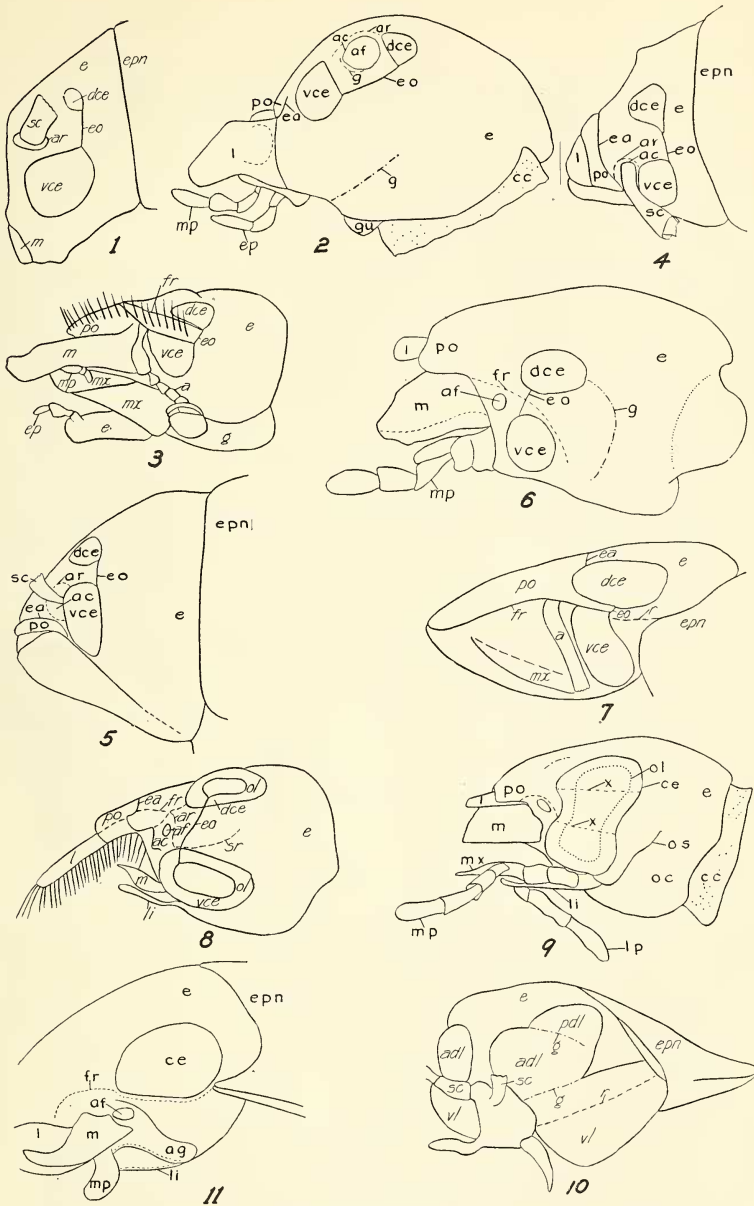
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## EXPLANATION OF PLATE XXVI

Figures 1-11: lateral aspect of heads of (1) *Euderces pini* Oliv., (2) *Tetraopes tetrophthalmus* (Forst.), (3) *Geotrupes splendidus* (Fab.), (4) *Polygraphus rufipennis* (Kby.), (5) *Xyloterinus politus* Say, (6) *Blapstinus metallicus* (Fab.), (7) *Amphiops gibbus mater* Sharp, (8) *Porrhorrhynchus landaisi* Rég., (9) *Colymbetes sculptilis* Harr., (10) *Dioptoma greeni* Gahan, (11) *Adelotopus dytiscoides* Newm.

Abbreviations: a, antenna; ac, antacava; adl, anterior dorsal lobe of compound eye; af, antafossa; ag, antennal groove; ar, antacaval ridge; ce, cervacoria; ce, compound eye; dec, dorsal compound eye; e, epieranium; ea, epicranial arm; eo, exoculata; epn, pronotum; fr, frontal ridge; g, groove or sulcus; gu, gula; l, labrum; li, labium; lp, labial palpus; m, mandible; mp, maxillary palpus; mx, maxilla; oc, occiput; ol, oculata; os, occipital suture; pdl, posterior dorsal lobe of compound eye; po, post-clypeus; r, ridge; sc, scape of antenna; sr, supraocular ridge; vee, ventral compound eye; vl, ventral lobe of compound eye; x, lines indicating possible homology between dorsal and ventral lobes of the eye of *Colymbetes* and dorsal and ventral eyes of gyrinid.



COLEOPTERA